

RESPONSE TO FIRE OF *CEANOOTHUS RODERICKII* (RHAMNACEAE),
A FEDERALLY ENDANGERED CALIFORNIA ENDEMIC SHRUB

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ABSTRACT

Experimental burns involving rare plants can provide important information for managers of those species. This study examined the response to prescribed fire of *Ceanothus roderickii*, a federally endangered chaparral species endemic to gabbro soils of the Pine Hill Formation in western El Dorado County, California. I conducted a laboratory study of germination cues, a field comparison of germination and survival on burned and unburned plots, and a comparison of seedling survival in burned plot subplots that were protected from vertebrate herbivores by wire exclosures. Seed germination was stimulated by heat (70° or 100° C) followed by a cold treatment. Burned plots contained 22-fold more seedlings than unburned plots, and seedling survival was significantly greater on burned plots. Exclosures significantly increased seedling survival on burned plots by 2 yr postfire. Plants on burned plots began to bloom and to branch layer (root at the nodes) by the sixth year postfire, with larger plants producing more fruits and being more likely to branch layer. I concluded that *C. roderickii* was similar to other species in the subgenus *Cerastes* in its obligate-seeding response to fire. However, its ability to branch layer enabled *C. roderickii* to increase plant density in burned plots, and thus continue postfire population recovery, long after fire-stimulated seedling establishment ceased. Branch layering by *C. roderickii* allows a postfire recovery pathway that is unique among species of obligate seeding *Ceanothus* studied to date.

Key Words: *Ceanothus*, chaparral, demography, endangered species, fire, gabbro, Pine Hill Formation.

Geology has a very important influence on plants (Kruckeberg 2002). In the western foothills of the central portion of California's Sierra Nevada, a small (104 km²) area of soils derived from a gabbro intrusion (the Pine Hill Formation) in western El Dorado County hosts a number of plants with limited or disjunct distributions (Hunter and Horenstein 1991; U.S. Fish and Wildlife Service 2002). Four of these are endemic to this formation: *Ceanothus roderickii* Knight; *Fremontodendron californicum* (Torrey) Cov. subsp. *decumbens* (R. Lloyd) Munz; *Galium californicum* Hook. & Arn. subsp. *sierrae* Dempster & Stebb.; and *Wyethia reticulata* E. Greene (Hunter and Horenstein 1991; U.S. Fish and Wildlife Service 2002). The restricted ranges of these species, along with rapid development of the area, have resulted in all but *W. reticulata* being listed as federally endangered (U.S. Fish and Wildlife Service 1996). All these species have populations growing on the Pine Hill Ecological Preserve, a 97 ha area established in 1979 to help protect these endangered species (U.S. Fish and Wildlife Service 2002).

Ceanothus roderickii was described by Knight (1968) as a prostrate or almost prostrate shrub in the subgenus *Cerastes*. It has suberect leaves and produces bluish-tinged flowers in late spring (Hickman 1993; U.S. Fish and Wildlife Service 2002). Fross and Wilken (2006) consider it closely

related to (and perhaps part of) *C. cuneatus*, a widespread species containing considerable variation. Knight (1968) mentioned that the prostrate branches of *C. roderickii* radiate from a central point (reminiscent of a wagon wheel) and that the branches tend to "arch" and root at the contact point of the arch. Thus, the shrub has a sprawling habit and can proliferate its rooting points through branch layering (rooting of branches). Of all California taxa of *Ceanothus*, Hickman (1993) reports only five others that root at the nodes, viz.: *C. confusus* J. Howell, *C. fresnensis* Abrams, *C. pinetorum* Cov., *C. prostratus* Benth., and *C. pumilus* E. Greene. To my knowledge the response to fire of these node-rooting species has not been studied.

As with many rare plant species, little ecological information is available for *C. roderickii* (U.S. Fish and Wildlife Service 1996). Thus, managers are hampered in their efforts to care for protected populations because this lack of information may prevent them from taking management actions for which the effects on the species are unknown. For example, the federally endangered maritime chaparral shrub *Arctostaphylos morroensis* Weisl. & Schreiber (Ericaceae) requires fire to stimulate seed germination but adult shrubs are killed by fire; prescribed fire may increase or decrease population size depending on the extent of seedling establishment (Odion and

Tyler 2002). Consequently, managers seeking to stimulate recruitment of this species via application of prescribed fire are gambling that adequate seedling establishment will occur to allow burned populations to recover. *Ceanothus roderickii* grows in openings in chaparral vegetation on the Pine Hill Formation (U.S. Fish and Wildlife Service 2002). Chaparral is a fire-adapted community and its plants possess various adaptations to fire (Keeley and Keeley 1988) but, prior to this study, the response to fire of *C. roderickii* was unknown.

In general, the post-fire response of chaparral shrubs differs between obligate seeders and sprouters (Keeley and Zedler 1978; Keeley and Keeley 1988). In obligate seeder species, shrubs are killed by fire and the population recovers via fire-stimulated recruitment from the seed bank. In sprouter species, shrubs resprout postfire and, for some species (i.e., facultative sprouters), additional individuals may be recruited from a persistent seed bank. The subgenus *Cerastes* of *Ceanothus* (to which *C. roderickii* belongs) contains obligate seeders and thus postfire population recovery of *C. roderickii* is expected to be similar to that of other species in this section. Typically, dense postfire seedling recruitment is modified by great mortality during establishment and thinning stages to result in a mature stand of plants about two decades postfire (e.g., Schlesinger et al. 1982). However, rooting of branches (branch layering), such as occurs for *C. roderickii*, may aid in postfire population recovery. Instead of a decline in density over time due to mortality of seedlings produced postfire, as has been shown for several obligate seeding *Ceanothus* species (e.g., Schlesinger et al. 1982; Zammit and Zedler 1993), *C. roderickii* populations may be able to increase density by branch layering when plants reach suitable size. However, the recent monograph on the genus by Fross and Wilken (2006) reports this species as "...reproducing entirely from seeds." The contribution of branch layering to postfire population recovery is thus in need of study.

Herbivory can greatly impact postfire growth and survival of chaparral plants (Davis 1967), including *Ceanothus* species (e.g., Bullock 1991). For example, Mills (1986) found that seedlings protected by exclosures had significantly greater survival and growth rates than those exposed to mammalian herbivores. He also reported that mammalian herbivores damaged seedlings differentially among shrub species: seedlings of *Ceanothus greggii* A. Gray were impacted by mammalian herbivory to a greater extent than those of chamise (*Adenostoma fasciculatum* Hook. & Arn). Thus, mammalian herbivore activity may be a factor important in postfire recovery of rare chaparral shrubs (such as *C. roderickii*) and deserves experimental assessment.

This study was designed to generate information regarding the effects of fire on *C. roderickii*. Its specific objectives were to determine: 1) if seed germination is stimulated by fire (using both lab and field studies); 2) if mature plants survive fire in the field; 3) some important demographic features of postfire recovery (plant size distributions, time to sexual maturity, time to rooting by the prostrate branches); and 4) the importance of mammalian herbivory to postfire population recovery.

METHODS

Study Site

This study was conducted at the Pine Hill Ecological Reserve, a conservation unit managed by the California Department of Fish and Game and centered on Pine Hill (elevation 628 m; 38°43' lat., 120°00' long.) in western El Dorado County, California. An area of about 1 ha along the top of the rocky ridge to the west of the summit was designated for a prescribed fire in the fall of 1984 (Boyd 2001). The burn was designed to test the responses to fire of three rare plant species found in this ecological reserve: *C. roderickii*, *Fremontodendron californicum* subsp. *decumbens* and *Wyethia reticulata*. Patches of *C. roderickii* were found in the open chaparral on the south-facing slope of this area. Plants were located in small open areas between shrubs and under shrub canopies (mainly *Arctostaphylos viscida* Parry with some *Adenostoma fasciculatum*).

Laboratory Germination Study

Seeds were collected in late June 1986 from dehiscing capsules produced by plants in unburned chaparral adjacent to the burn site. Because seeds of this federally endangered species were limited in quantity, this experiment examined the effects of heat and cold treatments sequentially rather than as independent factors. Fully formed, dark seeds were divided into three groups of forty seeds each. One group was not treated, the second was placed for 5 min in a forced convection oven heated to 70°C, and the third group was placed for 5 min into the oven heated to 100°C. Seeds from each treatment were divided into groups of ten seeds and each group was placed into a small (5 cm diameter) plastic Petri plate on a piece of filter paper moistened with de-ionized water. Petri plates were placed into a dark drawer kept at room temperature for 2 mo, at the end of which time any germination was noted. They then were placed into a coldroom (5°C) for 3 moths, after which they were removed and placed at room temperature for 2 wk. The number of germinating seeds (defined as emer-

gence of the radicle from the seed coat) was counted during that time. Effects of temperature treatments on germination were analyzed by Analysis of Variance (ANOVA) after log transformation of germinating seed numbers so that these count data would better meet the assumptions behind ANOVA (Zar 1996). Fisher's Probable Least Significant Difference (PLSD) test was used to compare means between temperature treatments (Abacus Concepts 1998).

Experimental Field Plots

All plots were located on the south-facing slope of the ridge upon which the prescribed fire was to be conducted. I selected nine 2×2 m plots with a relatively high cover of *Ceanothus roderickii* within the burn area, and nine similar plots outside the burn area, marking the corners of each with metal stakes. Plots were selected so that burned and unburned plots contained approximately similar densities of *C. roderickii*. To test this, I counted the number of rooting points (defined as a relatively discrete area of rooted branches) in each plot and compared the counts using a Mann-Whitney U test (Abacus Concepts 1998).

Most of the plots that had high *C. roderickii* cover in the burn area contained little fuel because the chaparral in that area had been cut in 1969 (Stebbins 1979) and had not recovered enough biomass to carry a fire. In order to apply fire uniformly to these plots, drying branches from shrubs cut during firebreak establishment were placed on these plots to a depth of about 0.75 m.

Maximum temperatures on the plots during burning were measured using temperature indicators made from temperature-indicating crayons (Omega Engineering, Stamford, CT). Melting points of the crayons used were 39, 59, 79, 87, 121, 142, 163, 184, 198, 226, 246, 288, 329, 343, 454, 550, 649, 760, 871, 982, 1090 and 1316°C. Temperature intervals between melting points of these crayons were approximately 20°C apart below 343°C and 110°C above. Each crayon was cut into small chips and one chip from each crayon was placed into an 8×4.5 cm envelope made of 1.4 mm-mesh steel screen. One of these temperature indicators was placed on the soil surface in the center of each burn plot before cut brush was piled onto the plots. Plots were burned 27 October 1983 (Boyd 2001). Conditions on the burn site were: relative humidity 36%, wind 0–6 kph and fuel moisture (measured with a 10-hr fuel stick) 7%. Temperature indicators were collected after the fire and the unmelted crayon pieces were used to determine the maximum soil surface temperature during the burning of each plot.

Response to Fire

Germination of *C. roderickii* in the burned plots was observed during the winter and spring of 1984. When emergence of new seedlings had slowed markedly (23 March 1984), I counted seedlings on each burned and unburned plot and, by periodic re-counting, followed their survival over the next two years. Plots were revisited at about monthly intervals until December 1984, every 1–2 mos during the winter and spring of 1985, once each in summer and fall of 1985, and once in the spring of 1986. The number of live plants from the 1984 cohort was counted each time, and during the late springs of 1985 and 1986 counts were made of additional seedlings in each plot that had germinated during the winter and spring of those years. Seedlings in burned plots that germinated in herbivore enclosure subplots (see description below) were excluded from this dataset. The few seedlings found in 1985 were marked with small bamboo stakes to allow their survival to be tracked independently from the 1984 cohort.

Surviving plants were measured during the second (1985) and sixth (1989) growing seasons after the fire to document the size structure of the population as well as to note the timing and extent of fruiting and branch layering. On 20 May 1985, 423 d after seedlings were first counted, I measured the size of each surviving plant in each burned plot. The length and width of each plant's canopy, measured as the longest dimension (length) and then the measurement of the canopy taken at right angles to the length (width), were recorded as well as the maximum height of the plant measured perpendicularly to the ground. These measurements were converted into canopy volumes (Boyd and Serafini 1992) using the formula for the height of a cylinder ($V = L \times W \times H \times \pi/4$). Four years later (17 June 1989), at the end of the sixth spring after the fire and 1913 d after seedlings were first counted, I revisited the burned plots and again measured the size of each surviving plant. In addition, for each plant I noted the number of mature fruits produced, whether any branches had rooted, and the distance from each crown to the rooting points of those branches. Plants in herbivore enclosures (see below) were excluded from these measurements.

Herbivore Enclosure Study

Wire mesh enclosures made of 5-mm mesh hardware cloth were used to exclude vertebrate herbivores from subplots in the burned plots. Enclosures were 25 cm long, 29 cm wide and 10 cm tall. Enclosed plots were matched with open plots of equal size by the following procedure. Two diagonal lines were established to

TABLE 1. COMPARISON OF PRE-FIRE ROOTING POINT AND POST-FIRE SEEDLING DENSITIES ON BURNED AND UNBURNED PLOTS. Data are means (SE), n = 9. P-values are the results of Mann-Whitney U tests comparing data from burned and unburned plots.

Parameter	Burned plots	Unburned plots	P-value
Rooting points (per m ²)	15.5 (1.7)	14.3 (1.0)	0.72
First year seedlings (per m ²)			
1984	24 (9.3)	1.1 (0.33)	0.0003
1985	0.25 (0.093)	1.1 (0.35)	0.052
1986	0.11 (0.085)	1.55 (0.53)	0.003

connect opposite corner markers of each plot. On the north side of each plot, one location along each diagonal line 40 cm from the corner marker was marked. If a location would make a poor experimental plot due to the presence of a large rock at the soil surface, the location was moved along the diagonal line until an area of exposed soil of suitable size was found. Once a pair of locations was marked, I flipped a coin to determine which would be covered by an exclosure and which would not. Exclosures were anchored to the ground by small (4 mm dia.) bamboo skewers and the corners of corresponding open plots (the areas of which were equal to those of exclosed plots) also were marked by bamboo skewers. A similar procedure was used to establish a pair of subplots (one exclosed and one open) on the south side of each plot. Subplots were established on 7 February 1984.

Seedlings were counted on 23 March 1984, after germination of *C. roderickii* had apparently ceased, and seedlings were recounted at approximately monthly intervals until December 1984. Afterward, I counted them at more sporadic intervals until 25 April 1986, more than two years from the start of seedling counts. Survival of seedlings in exclosures was compared to survival of seedlings in unexclosed plots using survival analysis (Abacus Concepts 1998), utilizing the Kaplan-Meier estimate with treatment significance determined by the Peto-Peto-Wilcoxon test at $\alpha \leq 0.05$ (Abacus Concepts 1998).

RESULTS

Laboratory Germination Study

Germination did not occur until seeds had been stratified. Seeds failed to germinate following the heat treatments after remaining for 2 mo at room temperature. However, after the cold treatment, seeds that had been heat-treated germinated rapidly (during 2 wk) and to similar extents. There was a significant temperature treatment effect (ANOVA; $F_{2,9} = 42$, $P < 0.0001$) because seeds that were not heat-treated did not germinate, even after stratification. Mean germination by seeds heated to 70°C was $38 \pm 2.5\%$ (SE) whereas germination by those heated to 100°C was $53 \pm 14\%$ (SE); these heat

treatment means were not significantly different (Fisher's PLSD test; $P = 0.38$).

Response to Fire

Burned and unburned plots had statistically equal densities of *C. roderickii* prior to burning, with mean densities of approximately 15 rooting points m⁻² (Table 1). Maximum temperatures recorded at the soil surface in burned plots were 980°–1316°C, with seven plots reaching 1090°C. All of the *C. roderickii* plants in burned plots were killed by fire.

Seedlings of *C. roderickii* occurred in both burned and unburned plots during 1984–1986. During the winter and spring of 1984, many seedlings (858) germinated on the burned plots and some (39) were found on unburned plots (Table 1). During the following two years, however, more seedlings were counted on unburned plots than on burned plots. Burned plots produced few seedlings after the initial flush of germinants in 1984 (Table 1). In 1985, unburned plots had 4-fold greater seedling density (Table 1), although this was only marginally statistically significant from seedling density on burned plots. In 1986, this difference increased and unburned plots contained significantly greater (14-fold higher) seedling density than burned plots (Table 1).

Survival of seedlings appearing on burned plots in 1984 was significantly greater than for seedlings germinating on unburned plots (Fig. 1; Peto-Peto-Wilcoxon rank test, $P < 0.0001$). Many seedlings in both types of plots appeared to have died from drought during late spring and early summer 1984 (judging by their wilted and shriveled appearance), whereas I noted vertebrate herbivore damage to some burned plot seedlings during June and July of 1984 and at some later census intervals. By 20 September 1984 (181 d after seedling monitoring began), only a single seedling remained alive in all unburned plots whereas burned plots contained a mean of 30 ± 13 (SE) seedlings. Some additional mortality also occurred in the burned plots after 20 September 1984 (Fig. 1). By April 1986 (763 d), 19% of plants on burned plots remained alive (Fig. 1) and by June 1989 (after 1913 d or 5.2 yr) 12% of plants on burned plots were alive.

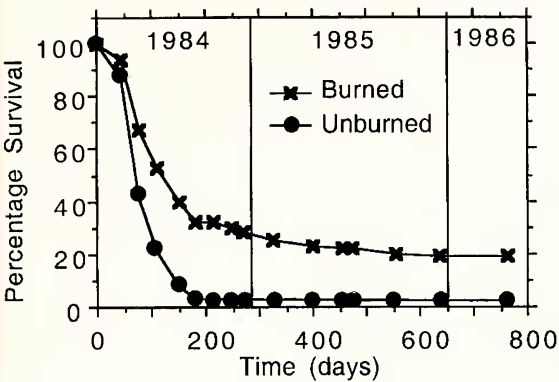


FIG. 1. Survival of seedlings on burned and unburned plots from 23 March 1984 until 25 April 1986. Time in days is measured from 23 March 1984, at which time 858 seedlings were counted on burned plots and 39 on unburned plots.

Within the burned plots, 98.5% of all seedlings found during 1984–1986 germinated the first season postfire (1984). Seedling survival on burned plots varied greatly among plots. Despite all burned plots having roughly similar numbers of rooting points prefire (range 32–91), by 1989 two plots had only one surviving plant and another had just two. Many (64, or 66%) of the 97 plants surviving in 1989 were concentrated in just two of the burned plots. There was little correlation between the prefire count of rooting points and the number of plants counted on burned plots in 1989 (simple linear regression, $r^2 = 0.034$): for example, the plot with the greatest prefire count of rooting points (91) contained just two plants in 1989.

Plants on burned plots in May 1985 were relatively small (Fig. 2), but the single unburned plot plant still alive from the 1984 cohort was 0.001 dm^3 in volume and equaled some of the smallest of the burned plot seedlings. Plants in burned plots had grown rapidly by 1989 (Fig. 2) so that mean plant size ($11 \pm 1.3\text{ dm}^3$ [mean $\pm 1\text{ SE}$]) was 145-fold that of plants measured in May 1985 ($0.076 \pm 0.0078\text{ dm}^3$).

One plant in the burned plots fruited in 1988. In 1989 (six seasons post-fire), many plants on the burned plots (33%) produced at least one fruit. Fruit production per plot in 1989 varied widely (0–280) and there was a strong positive relationship between number of plants per plot and fruit production per plot (linear regression; $F_{1,7} = 34$, $P = 0.0006$, $r^2 = 0.81$). For convenience, I arbitrarily divided 1989 plants into five size classes (0–10, 10–20, 20–30, 30–40, and $> 40\text{ dm}^3$) to investigate the influence of plant size on fruiting and branch layering. The proportion of individuals fruiting varied significantly with plant size (contingency table analysis; $\chi^2 = 26$, $df = 4$, $P < 0.0001$) and fruiting was concentrated among the larger size classes of

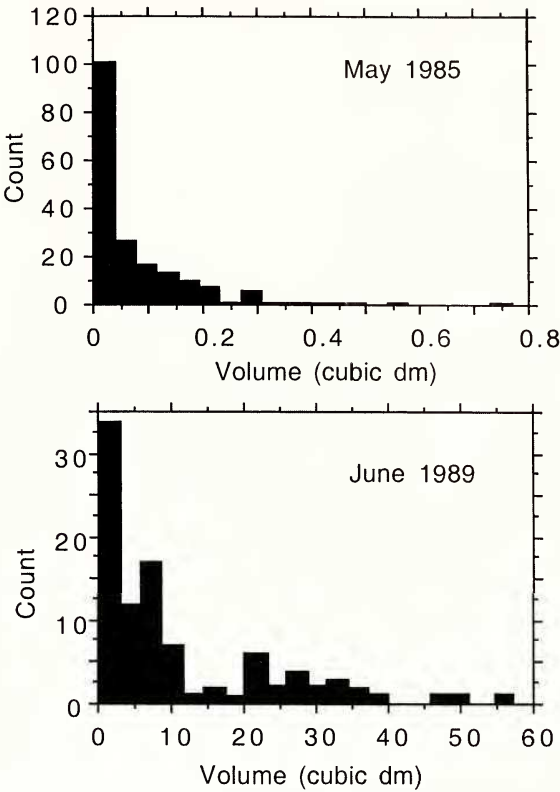


FIG. 2. Size distributions of plants (in dm^3) on burned plots in May 1985 (during the second growing season postfire) and June 1989 (during the sixth season postfire).

plants (Table 2). Only 19% of the many relatively small plants ($< 10\text{ dm}^3$) produced fruits, whereas at least 38% of the plants in the larger size classes produced fruits (Table 2). The number of fruits produced by each plant also increased significantly with plant size (linear regression; $F_{1,95} = 14$, $P = 0.0003$), although the relationship was rather weak ($r^2 = 0.13$).

Rooting of the longer branches of some plants was observed in 1989. At that time, 23% of the 97 plants surviving outside of exclosures had pro-

TABLE 2. DISTRIBUTION OF FRUITING INDIVIDUALS AND THOSE PRODUCING ROOTED BRANCHES AMONG THE SIZE CLASSES (DIVIDED BY CANOPY VOLUME IN dm^3) OF *C. RODERICKII* PLANTS FOUND ON THE BURNED PLOTS IN JUNE 1989. Inds. = individuals.

Size class (dm^3)	n	Fruiting (% of inds.)	Production of rooted branches (% of inds.)
0–10	67	19	10
10–20	7	57	29
20–30	13	38	46
30–40	7	100	86
> 40	3	100	33

duced at least one rooted branch (15 plants with one rooted branch, and 7 with more than one rooted branch). Not surprisingly, production of rooted branches varied significantly with plant size (contingency table analysis; $\chi^2 = 26$, $df = 4$, $P < 0.0001$) and was concentrated in the larger size classes of plants (Table 2). Inspection of Table 2 shows that the smallest size class had relatively few plants producing rooted branches (10%), whereas many plants ($\geq 29\%$) in the 20–30 and 30–40 dm^3 size classes were producing rooted branches by 1989. Altogether, rooting of branches contributed close to a third (27%) of the rooting points counted outside of the herbivore exclosures in the burned plots in June 1989. In addition, a number of larger plants had at least one arching branch touching the soil, and likely soon formed rooting points.

Comparison of rooting points in each plot postfire against the number counted prefire provides a measure of the degree of recovery of the burned plot populations. By June 1989, only one burned plot contained more rooting points than it had contained prefire. Most of the other plots had very few rooting points: three plots had just 1 or 2. The 1989 density of rooting points per plot was 3.8 ± 1.5 (SE). This was 25% of the prefire mean value of 15.5 (Table 1) and was significantly less than the prefire rooting point density (paired t-test: $t = 4.8$, $df = 8$, $P = 0.0014$). However, the contribution of branch layering to rooting point density was important for some plots. When April 1986 counts of surviving plants were compared to June 1989 counts of rooting points, four of the nine plots showed increases in rooting point counts in 1989. Because germination and seedling establishment had ceased on burned plots by 1986, this increase in rooting points indicated that branch layering had begun to reverse decreases in plant density that occurred during the first several postfire seasons because of mortality of individual plants (e.g., Fig. 1).

Herbivore Exclosures

Seedlings protected by exclosures had higher survival rates than those in open plots (Fig. 3). Most plants in either treatment category died during the late spring and summer of the first year (days 46–211, Fig. 3). Many of these dead plants were noted standing dried but intact and probably were killed by drought. During visits after 20 August 1984 (day 150), I noted damage by vertebrate herbivores (clipping of stems) to plants in open plots and one case of the burial of a plant by activities of a pocket gopher. The loss of these plants contributed to the decline in survival of open plants during that time (days 150–250), whereas most exclosed plants survived during that period (Fig. 3). By the second spring

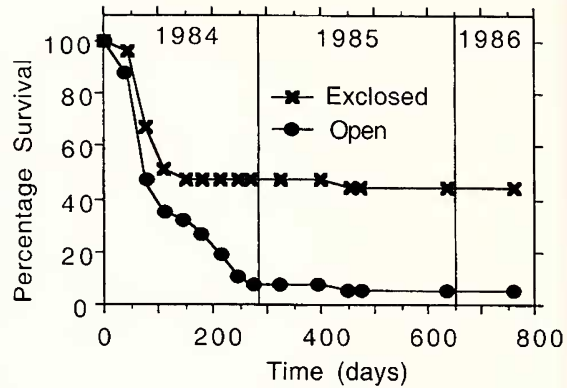


FIG. 3. Survival of seedlings in exclosed or open subplots of burned plots from 23 March 1984 until 25 April 1986. Time in days is measured from 23 March 1984, when 45 seedlings were counted in exclosed plots and 37 in open plots.

after the plots were burned (20 May 1985, day 423), 44% of exclosed plants had survived in contrast to just 5% of open plot plants. Survival analysis showed the two groups of plants differed significantly in their survival patterns (Peto-Peto-Wilcoxon rank test, $P = 0.0016$).

DISCUSSION

Fire killed mature plants of *C. roderickii* and stimulated seed germination. The failure of burned mature plants to resprout is consistent with reports for other species in the subgenus *Cerastes* (e.g., Keeley and Zedler 1978; Keeley and Keeley 1988).

Stimulation of seed germination by heat from fire is also unsurprising: Keeley (1991) listed 24 species of *Ceanothus* for which germination is stimulated by heat. My results also suggest that seeds of *C. roderickii* require stratification for germination, which has been shown for some species of *Ceanothus*, and previously reported for *C. roderickii*. Studies of certain other *Ceanothus* species, e.g. Quick (1935) and Bullock (1982), have shown that heat treatment followed by cold ($< 2.5^\circ C$) gives greatest germination. Also, James (1996) reported that *C. roderickii* germinated best when treated by heat followed by cold conditions. In my laboratory study, seeds germinated only after heat treatment was followed by stratification. Although did not contain a stratification-no heating treatment, seedlings were found in the field in late winter and spring, which also is consistent with a stratification requirement for *C. roderickii* germination.

Some germination occurred in control plots each year, however, showing that germination is not completely dependent on fire. Limited germination of other *Ceanothus* species in unburned chaparral stands has been reported

(Keeley 1992), either because soil surface temperatures on open sites in summer are sufficient to stimulate germination of some seeds (Keeley and Keeley 1981) or because a small percentage of seeds are nonrefractory (Keeley 1987). However, establishment of *Ceanothus* is generally limited to postfire conditions as seedlings germinating in unburned chaparral usually die (Keeley 1992). That was the case in this study (Fig. 1).

Despite the germination of seedlings each season in plots that were not burned, recruitment was almost completely limited to seedlings in plots that had been burned during the first postfire season (Fig. 1). Thus, changes in site conditions that follow fire (e.g., increased soil nutrients, decreased competition from other plants) likely aid successful seedling establishment. This is consistent with other *Ceanothus* species discussed by Keeley (1991), in which recruitment generally occurs from seeds that germinate in the first season postfire, despite some seeds germinating in second or later postfire seasons.

Mortality of *C. roderickii* seedlings on burned plots was greatest in the first season postfire (Fig. 1). This result is similar to that of many other chaparral studies of postfire seedling demography (Keeley and Keeley 1988). For example, Kummerow et al. (1985) documented 92% mortality of *C. greggii* seedlings during the first postfire growing season. That study, as well as others such as Thomas and Davis (1989), Moreno and Oechel (1992), and Tyler and D'Antonio (1995), provide further evidence that water availability limits postfire *Ceanothus* seedling survival. The shriveled yet undamaged appearance of most dead *C. roderickii* seedlings in my study also implied drought as a major mortality factor. It has been suggested that seedlings of seeder plant species are more drought-tolerant than those of sprouters (Parker 1984), but a recent study by Schwilk and Ackerly (2005) found no evidence of differential drought tolerance of obligate seeder compared to sprouter *Ceanothus* species.

Herbivory was a secondary cause of *C. roderickii* mortality. Although some herbivore damage was observed during the summer of 1984, most herbivore damage (apparently browsing by mammals) was observed in the second postfire season (1985). By the end of the second season, seedlings in exclosed subplots were significantly longer-lived than those in open plots (Fig. 3). Although there was no control (open sided) exclosure treatment that allowed me to explicitly separate the shading effect of an exclosure from its protective effect against herbivory (e.g., Martens and Boyd 2002), observations of browse damage to plants in open subplots support the interpretation that herbivore damage in those subplots was a major contrib-

utor to plant mortality. This result is similar to that of Mills (1986), except that he found significant insect herbivory in addition to significant effects of mammalian herbivores. Insect herbivory also was reported as a significant factor in postfire survival of *C. greggii* (Moreno and Oechel 1992). In my study, I noticed insect damage to fruits of *C. roderickii* but not major damage to foliage.

As with many plants (Klinkhamer et al. 1997), including some species of *Ceanothus* (e.g., Zammit and Zedler 1993), fruit production was greater by larger *C. roderickii* plants. Branch layering also was more likely to occur for larger *C. roderickii* plants. This fact emphasizes the importance of larger *C. roderickii* individuals to population recovery as they are able to both contribute more seeds to the seed bank and increase rooting point density through branch layering.

Keeley (1992) pointed out that seeder species generally have single aged cohorts of stems, whereas resprouters may have multiple age stems on individual shrubs. Although my data confirm *C. roderickii* as a seeder species, its branch layering ability allows it to add stems (via branch layering) to its population long after postfire seedling establishment ends. For *C. roderickii*, branch layering was first documented in the sixth season postfire. It probably accelerated in subsequent seasons, as smaller plants grew branches long enough to root and as branches with one rooting point added additional rooting points. One consequence was that, unlike other seeder species, the density of *C. roderickii* (as measured by rooting points per unit area) began to increase in some plots once branch layering began. Thus, postfire recovery of *C. roderickii* populations covers a much longer timeframe than for *Ceanothus* species that do not branch layer. In contrast to other *Ceanothus* species studied to date, population density of *C. roderickii* is not determined solely by germination followed by postfire seedling mortality. For example, one of the burned plots had 74 rooting points prefire and produced 36 seedlings in 1984, but by 1986 only 4 plants remained. However, in June 1989 branch layering had resulted in a count of 8 rooting points on that plot, doubling the plot's rooting point density. It is interesting to note that *Arctostaphylos*, another dominant California chaparral genus that contains both seeder and sprouter species (Keeley and Keeley 1988), contains several low-growing (prostrate to spreading) taxa that are reported to root at the nodes (Hickman 1993): *A. hookeri* G. Don subsp. *hearthiorum* (Hoover and Roof) P. Wells; *A. parryana* Lemmon; and *A. patula* E. Greene. Some populations of *A. patula* are reported to resprout following fire (Wells 1968) and thus may have a mix of traits (sprouting and branch

layering) that could represent a unique postfire recovery strategy.

The results of this study have application to rare species management. When this study was conducted, the response of *C. roderickii* to fire was unknown and hence managers of the Pine Hill Ecological Reserve were reticent to conduct a prescribed burn. Because this study showed that *C. roderickii* germination is stimulated by fire and therefore populations can recover, that burn took place. This leads to the question of how often such burns should be conducted to maintain the chaparral on the Pine Hill Reserve. As a seeder species, *C. roderickii* depends on recruitment from the seed bank in order to re-establish populations after fire. Keeley and Keeley (1988) state that obligate seeding species require 5–15 yr to produce substantial seed crops. This is probably the case with *C. roderickii*, for which notable flowering and fruit production occurred in the sixth season postfire (1989, when about one-third of plants flowered). Although replenishment of the seed bank probably began at that point, it is unknown how long it takes to return the *C. roderickii* seed bank to adequate levels for postfire stand regeneration. Seed predation by mammals and birds probably destroys considerable numbers of the seeds produced by chaparral shrubs (Keeley 1977; Davey 1982; Kelly and Parker 1990; Boyd and Serafini 1992; O'Neil and Parker 2005). Furthermore, studies of other chaparral species imply that fires themselves cause considerable mortality of seeds in soil (Keeley 1977; Odion 2000; Odion and Davis 2000; Odion and Tyler 2002). Thus, it seems prudent to allow *C. roderickii* populations sufficient time to adequately build up the seed bank before another prescribed fire is conducted on the Pine Hill Ecological Reserve.

Odion and Tyler (2002) also proposed a long postfire recovery period for the federally endangered *Arctostaphylos morroensis*, an obligate seeder species that may need more than four decades to build up a seed bank adequate to replace the prefire population. However, a crucial difference between *C. roderickii* and *A. morroensis* is the branch layering ability of *C. roderickii*. Odion and Tyler (2002) found that high postfire seedling mortality of *A. morroensis* reduced recovering population density to less than that of the original stand. As a result, the new *A. morroensis* population was significantly smaller (< 50% by 3 yr postfire) than the original: the prescribed burn resulted in a net loss of individuals of this endangered species. In my study, by 1986 seedling mortality had reduced plant density (rooting points) to below prefire levels in all but one plot (overall *C. roderickii* density was 25% of that prefire). However, the branch layering ability of *C. roderickii* allowed density to increase between 1986 and 1989 in four

plots. Plant numbers on all plots rose from 136 (in 1986) to 138 (in 1989) despite mortality of 29% of plants between 1986 and 1989. By 1989, branch layering had produced 27% of the rooting points counted and branch layering was just beginning at that time. Continuation of branch layering should enable *C. roderickii* to continue recovery toward prefire densities in most if not all plots. This illustrates the importance of branch layering to postfire recovery of this federally endangered obligate seeding chaparral species.

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